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FUNCTIONAL SIGNIFICANCE OF THE SEXUAL DIMORPHISM IN THE CEPHALIC APPENDAGES OF *EUCHAETA RIMANA* BRADFORD

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ABSTRACT

In *Euchaeta rimana* the cephalic appendages become profoundly sexually dimorphic at the final molt. The enlarged maxillipeds and robust maxillae, which are related to the predatory nature of this pelagic marine copepod are fully functional on the fifth copepodid (CV) males and adult females. The presumed prey detection sensory apparatus, a paired 4-point setal array on the antennules, is located within the capture volume of the feeding current of the CVs and adult females. SEMs reveal specialized basal articulations of the straight and curved setae of this array, that allow setal rotations that streamline the antennule during escape movements. In the final molt of the CV male to the adult stage, the maxillae are reduced to vestiges and the maxillipeds to half the size of the female's. The loss of functional prey capture appendages is accompanied by the loss of the prominent antennulary setal array, giving support for their postulated function as prey sensors. Instead, the male gains 19 more aesthetascs primarily in the proximal region of the antennules, where fluid velocities of the scanning current are greatest. Detection of pheromones transported within the feeding/scanning current is the hypothesized function of the chemosensory system of the adult male copepod. The parallel changes in the structure of the antennule as well as of the adjacent cephalic appendages suggest that a homeobox-like gene control system could be coordinating these morphological changes.

Sexual dimorphism in the antennules of copepods has long been recognized in calanoid and other copepods (Jurine, 1820). In *Euchaeta* Philippi and *Pareuchaeta* Scott species the conspicuous setation differences between male and female antennules have been reported on by Claus (1863), Giesbrecht (1892), Sars (1903) and many others. More recently Yen and Nichol (1990) described in detail the 4-point, 3-dimensional array of elongate setae on the antennules of female *Pareuchaeta norvegica* (Boeck) and noted that males of *Euchaeta* lose these elongate setae at the final molt from fifth copepodid to adult. Yen and Nichol also reported that the 3-dimensional array of females is common to at least four species of euchaetids.

In a comparative study of representatives of all copepod orders Huys and Boxshall (1991) developed a system for identifying homologous segments in the antennules. This system is a development of Giesbrecht's (1892) trithek scheme in which he attempted to derive all copepod antennules from a common 25-segmented pattern. The discovery of copepods with 26 (Scott, 1901, Huys and Boxshall, 1990) and 27 antennulary segments (Fosshagen, 1970) had demonstrated that Giesbrecht's system was in need of revision (Boxshall, 1983). Huys and Boxshall's (1991) analysis of the antennulary segmentation indicated that a total of 28 segments is expressed in modern copepods although all known species exhibit some fusion between these ancestral segments. The use of a dual numbering system (Huys and Boxshall, 1991) permits the identification of homologous segments independent of any segmental fusions.

This paper documents in detail the changes in antennulary structure and setation that occur at the molt between fifth copepodid male and adult male. Yen and Nichol (1990) reported that the 4-point array of long setae in female *Euchaeta rimana* Bradford is aligned

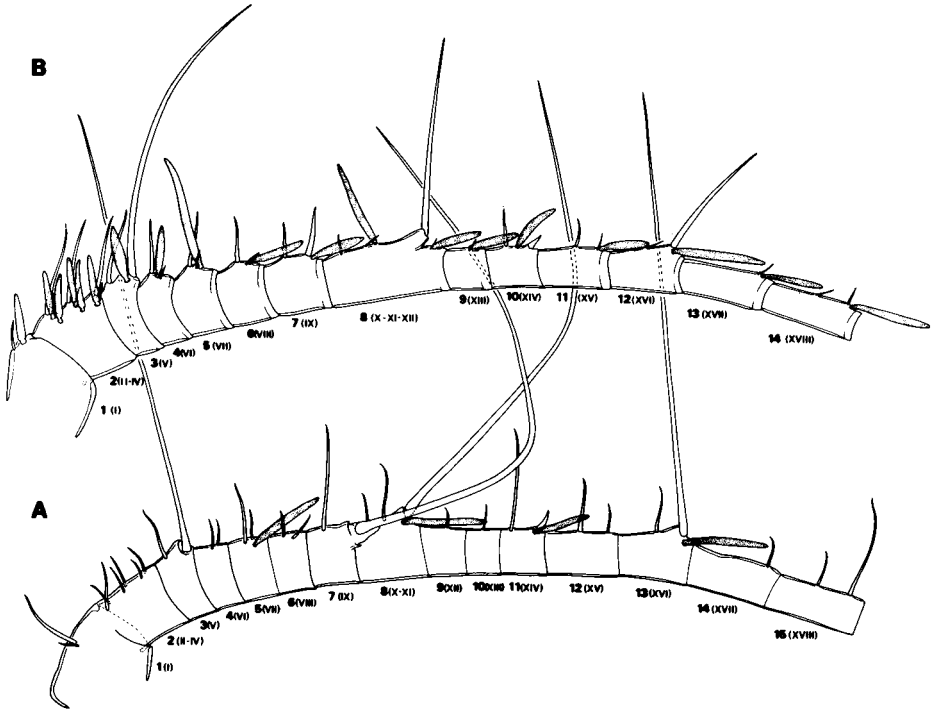

Figure 1. *Euchaeta rimana*. A: Proximal 15 segments (I to XVIII) of antennule of adult female. B: Proximal 14 segments (I to XVIII) of antennule of adult male. Stippled elements are aesthetascs; Roman numerals indicate ancestral segmental homologies; Arabic numerals indicate actual segments.

parallel to the flow field created by the motions of the other cephalic appendages so the profound changes in these appendages that occur at the same molt are also briefly documented here, since they may influence the flow regime over the antennulary sensors.

Materials and Methods

Adults of both sexes and fifth copepodid stage males were collected at the Natural Energy Laboratory of Hawaii, using plankton nets placed over the outflow of a pipe drawing near surface water from off Ke'ahole Point, Kailua Kona, Hawaii Island. Specimens for light microscopy were initially fixed in 10% neutral buffered formalin and examined, as temporary whole mounts or after dissection, in lactophenol. Drawings were made using a camera lucida on a Leitz Diaplan microscope equipped with Differential Interference Contrast. Material for scanning electron microscopy (SEM) was fixed in 2.5% glutaraldehyde, post-fixed in Osmium tetroxide, dehydrated through graded acetone, critical point dried, then mounted on stubs and sputter coated with gold. SEM observations were made using a Hitachi S800 microscope.

The dual numbering system for antennulary segments proposed by Huys and Boxshall (1991) is adopted here: actual segment numbers are indicated by Arabic numerals and ancestral segment numbers are indicated by Roman numerals. So, for example, segment 2(II-IV) indicates that the second segment of the expressed antennule is derived from the second to fourth ancestral segments.

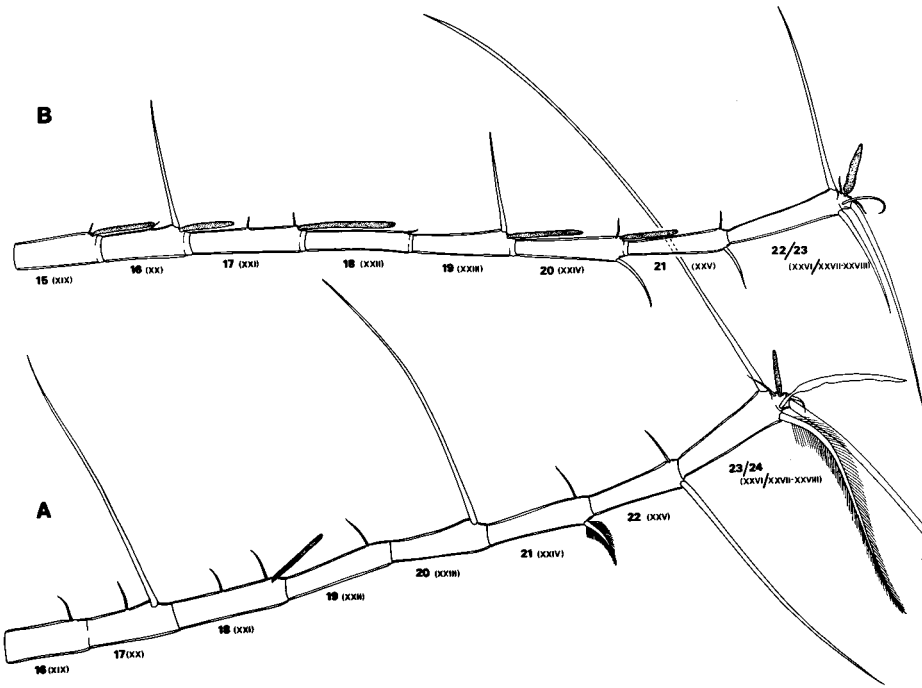

Figure 2. *Euchaeta rimana*. A: Distal part of antennule of adult female. B: Distal part of antennule of adult male. Numbers as for Fig. 1.

RESULTS

ANTENNULES OF ADULT FEMALE AND FIFTH COPEPODID MALE. — The antennules of the fifth copepodid male and the adult female (Figs. 1A, 2A) are symmetrical and apparently 23-segmented. They are similar in segmentation except that in the fifth copepodid several of the segmental articulations are incompletely expressed. In both stages segments 1 (I) and 2 (which is a triple segment derived from ancestral segments II-IV) are partly fused. Segments 3 (V) to 7 (IX) are separate. Segment 8 is a double segment derived from ancestral segments X and XI. Segments 9 (XII) to 22 (XXV) are separate, although some are incompletely so in male fifth copepodids. Segment 23/24, the apical segment, appears to be divided into a large segment 23, representing ancestral segment XXVI, bearing a long anterior seta and a long, plumose posterior seta, and a very short segment 24 (Fig. 3A) representing segments XXVII and XXVIII, which are fused in all neocopepodan copepods. However, this subdivision which is shown as an integumental fold under scanning electron microscopy (arrowed in Fig. 3A) is not readily visible using light microscopy and may not represent a functional articulation.

The setation patterns of the fifth copepodid male and adult female are identical. Important characteristics of this pattern are: the retention of aesthetascs on segments 5 (VII), 8 (XI), 11 (XIV), 13 (XVI), 18 (XXI) and 23/24 (XXVII-XXVIII); the loss of 1 seta from segments 8 (X-XI), 9 (XII), 10 (XIII), 14 (XVII) and 16 (XIX); the presence of a stout

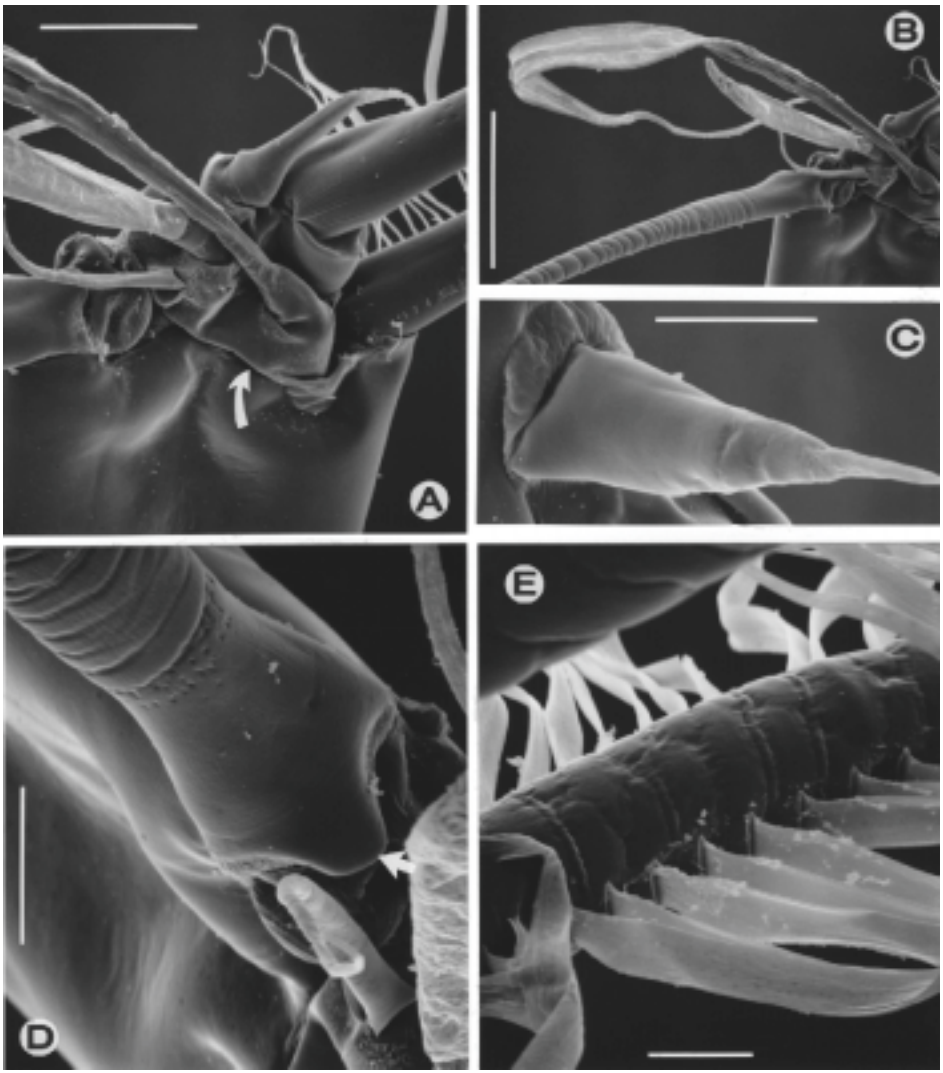

Figure 3. *Euchaeta rimana.* A: Apex of female antennule, showing apical segment (XXVII-XXVIII) bearing five elements, partly defined from preceding segment (XXVI) by integumental fold (arrowed). B: Same, showing detail of whip seta and aesthetasc. C: Spine on segment 11 (XIV). D: Basal articulation of long, anteriorly-directed seta on segment 23 (XXVI), showing typical grooved surface of long setae and process (arrowed) on setal base. E: Detail of posterior seta on segment 21 (XXIV), showing flattened pinnules of plumose seta. Scale bars A = 20 μm, B = 43 μm, C = 7.5 μm, D = 10 μm, E = 5 μm.

spiniform element on segment 11 (XIV) (Fig. 3C); and the retention of posterior margin setae on segments 21 (XXIV), 22 (XXV) and 23/24 (XXVI). The short apical segment carries 1 very long, posteriorly-directed seta, 2 short setae, the whip seta (Fig. 3B) and an aesthetasc.

The main feature of each antennule is the 3-dimensional array of 4 long setae in the proximal part of the limb (Fig. 4A). The long setae on segments 3 (V) and 13 (XVI) are

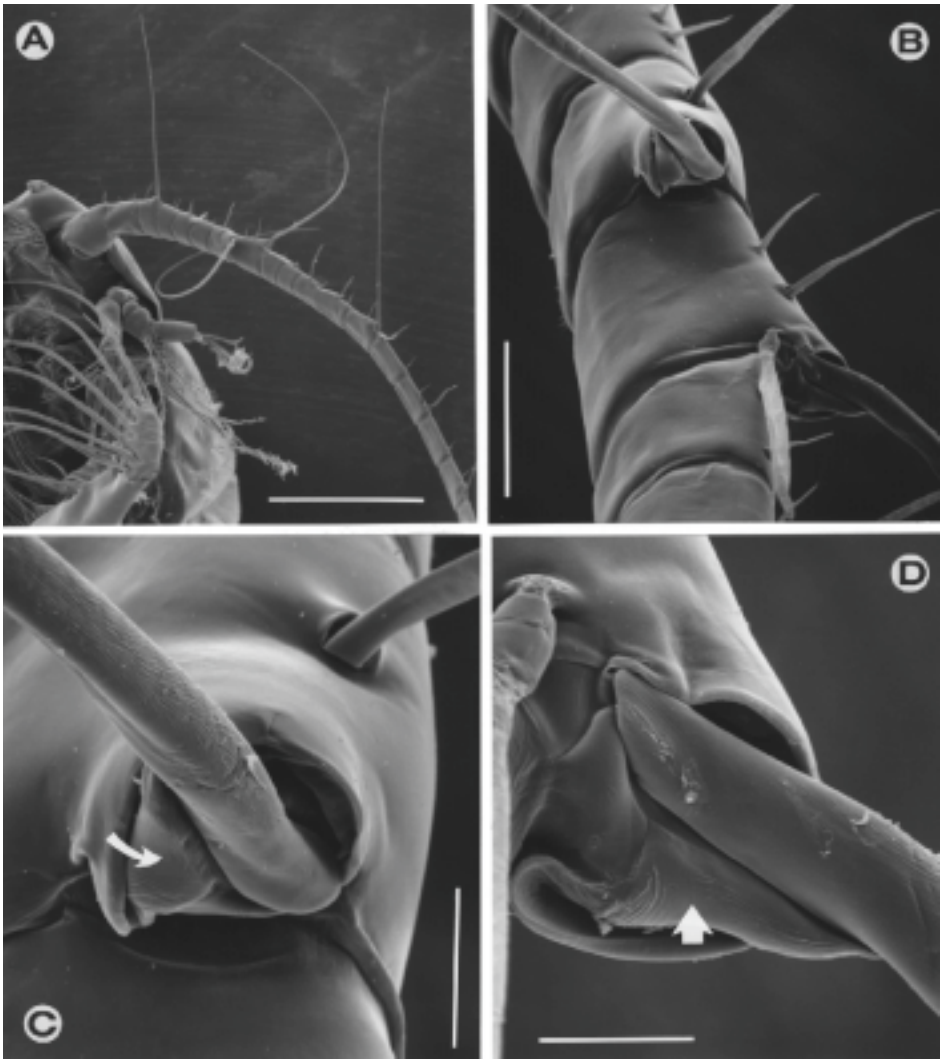

Figure 4. *Euchaeta rimana*. A: Ventral view of proximal part of adult female antennule, showing 3-dimensional array of long setae. B: Detail of segments 7 (IX) and 8 (X-XI), showing ventrally and dorsally directed long setae. C: Basal articulation of long seta on segment 7 (IX), with arrow indicating triangular integumental pad within socket. D: Basal articulation of long seta on segment 8 (X-XI), with arrow indicating integumental pad within socket. Scale bars A = 430 μm, B = 60 μm, C = 20 μm, D = 15 μm.

straight and directed anteriorly. Those on segments 7 (IX) and 8 (X-XI) are strongly curved; that on segment 7 passing ventrally before curving anteriorly, that on segment 8 passing dorsally before curving anteriorly. The tips of these four setae project forward and are equidistant from the face of the antennule, as shown for *P. norvegica* by Yen and Nichol (1990). Long or medium-length setae are also found anteriorly on segments 17 (XX), 20 (XXIII) and 23/24 (XXVI), and posteriorly on segments 22 (XXV) and 23/24

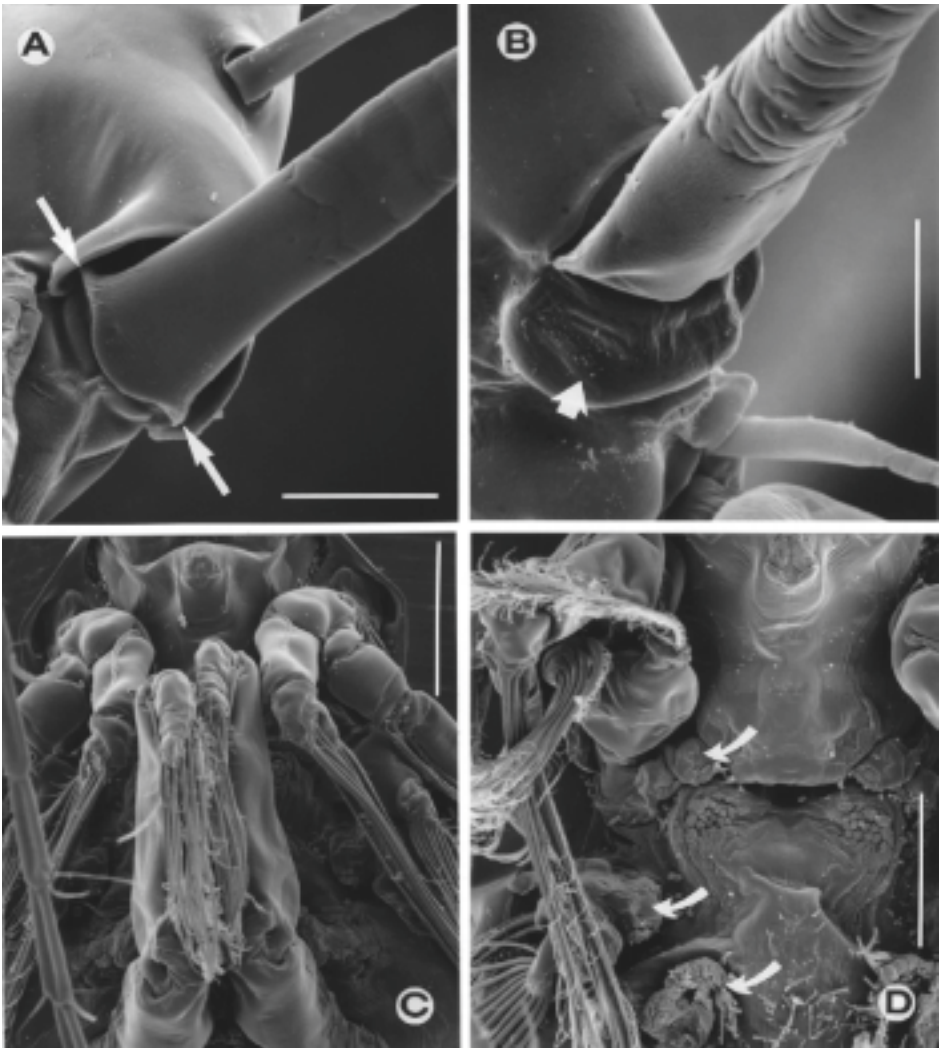

Figure 5. *Euchaeta rimana.* A: Basal articulation of long seta on segment 13 (XVI) of female antennule, with arrows indicating pivots of hinge line around which rotation of seta occurs. B: Basal articulation of long, anteriorly-directed seta on segment 23 (XXVI) of female antennule, with arrow indicating swelling distal to base that prevents over-rotation of seta. C: Ventral view of oral region of adult male, showing orientation of maxillipeds. D: Same, with maxillipeds removed, showing reduced labrum and mouth opening, with arrows indicating reduced mandibular gnathobase, reduced praecoxal arthrite of maxillule and entire maxilla. Scale bars A = 15 μm, B = 7.5 μm, C = 200 μm, D = 150 μm.

(XXVI and XXVII-XXVIII). The posterior margin setae of segments 21 (XXIV) and 23/24 (XXVI) are plumose (Fig. 3E).

The articulations between the long setae and the segments of the female antennule are specialized. The basal articulations of the long straight setae on segments 3 and 13 (Fig. 5A) are similar. Each seta can move in one plane only, about a transverse pivot line the ends of which are indicated by the arrows in Figure 5A. The proximal swing of the seta is

restricted by the expanded semicircle of integument proximal to the setal base. The seta is able to swing distally so that it lies flat along the antennule with its tip directed toward the apex of the limb. The smaller seta located on the same segment exhibits a similar basal articulation permitting the seta to swing in one plane only and restricting the movement to the distal quadrant. This type of articulation is the basic type observable in the majority of the setae along the antennule, irrespective of length.

The basal articulations of the long curved setae on segments 7 and 8 are modified (Fig 4B). The seta on segment 7 is directed ventrally. Proximal to its basal articulation lies an expanded semicircle of integument preventing proximal movement of the seta but the seta is not located symmetrically in the center of this semicircular socket. Its base is located toward the dorsal part of the socket and there is a triangular integumental process (arrowed in Fig. 4C) filling the space between seta and socket ventrally. The dorsally directed seta on segment 8 has a very similar articulation, except that the seta is located ventrally in its asymmetrical socket and the triangular integumental process (arrowed in Fig. 4D) fills the space between the seta and the socket dorsally.

ANTENNULES OF ADULT MALE. — The antennules of the adult male (Figs. 1B, 2B) are symmetrical, apparently 22-segmented and exhibit the following fusions: segment 2 represents fused ancestral segments II to IV, and segment 8 represents fused ancestral segments X to XII. Segment 22 appears partly subdivided into a long segment 22 (XXVI) and a minute apical segment representing fused segments XXVII to XXVIII. As in the female and male fifth copepodid, the separation of the apical segment is ambiguous.

The setation pattern differs markedly from that of the fifth copepodid male (cf. Fig. 1A, 2A). Apart from the loss of a single seta from the first segment, the change in number of elements from fifth copepodid to adult is the addition of 19 aesthetascs. These additional aesthetascs are distributed along the antennule from the first to the 20th segments, although the greatest density of additional aesthetascs is in the proximal few segments (Fig. 6A). The aesthetascs on segments 5 (VII) and 8 (that from segment XI) (Fig. 6E) are larger than the homologous elements on the female antennule, and both are anteriorly-directed rather than lying more parallel with the limb axis as in the female. The terminal aesthetasc is more robust in the adult male than in the copepodid and the female.

The most obvious change in the pattern of antennulary setae is the loss of the 3-dimensional array of long setae (Fig. 6B) described above for the fifth copepodid male and adult female (Fig. 4A). The long seta on segment 3 (V) of the fifth copepodid remains (Fig. 6B, C), although it is characteristically curved distally and has an apical pore (Fig. 6D). The distal seta on segment 7 (IX) is short and directed anteriorly rather than ventrally. The long seta on segment 8 (XI of triple segment X-XII) is directed anteriorly rather than dorsally (Fig. 6E). Finally, the distal seta of segment 13 (XVI) is much shorter. The anterior setae on segments 16 (XX), 19 (XXIII) and 22 (XXVI), and the posterior setae on segments 21 (XXV) and 22 (XXVI) are also relatively shorter than their homologues in the fifth copepodid and female. As in the fifth copepodid and female a short spiniform element is present on the segment derived from ancestral segment XIV. The posteriorly-directed setae on segments 20 (XXIV) and 22/23 (XXVI) are naked rather than plumose as are the homologous elements in the female. The setation of the minute apical segment also differs markedly from the fifth copepodid stage. The posteriorly-directed long seta is much shorter and the whip-like element of the fifth copepodid male resembles an unmodified seta in the adult.

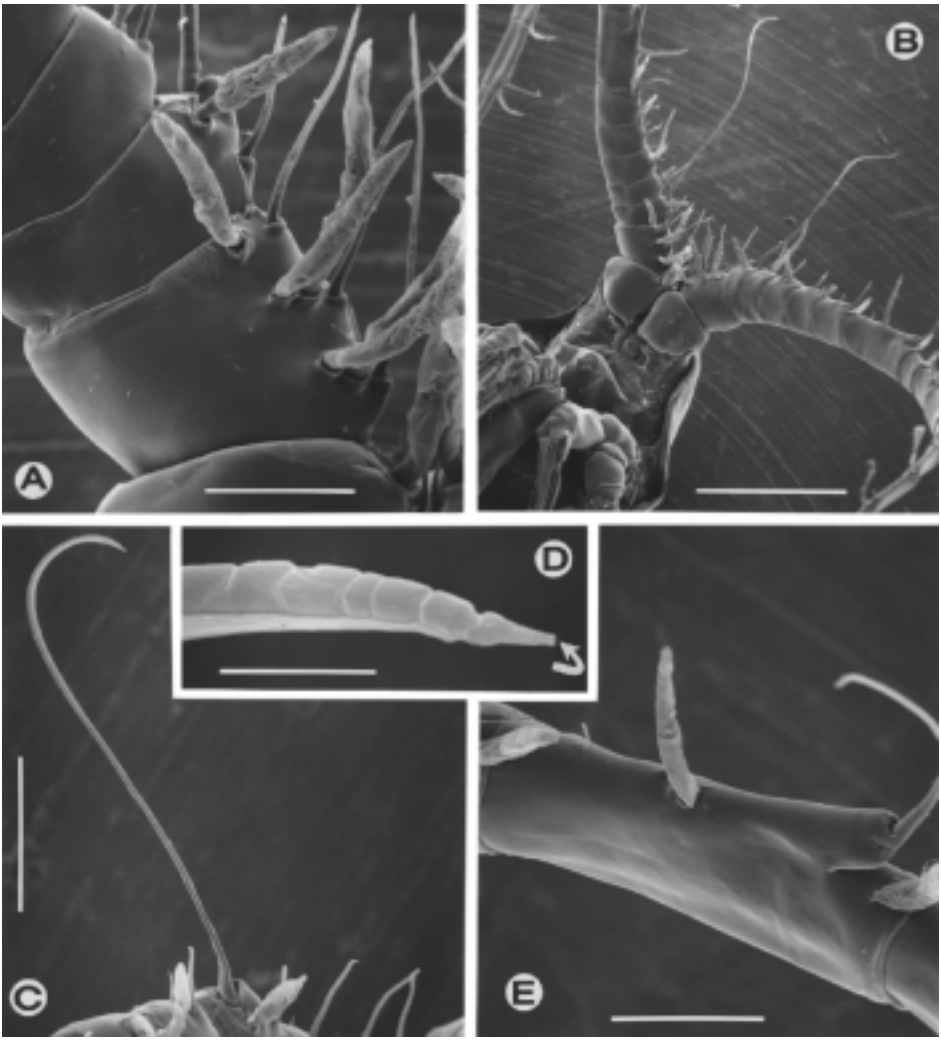

Figure 6. *Euchaeta rimana.* A: Ventral view of proximal part of male antennule, showing double aesthetascs on second segment. B: Ventral view of male showing proximal parts of antennules. C: Long seta on segment 3 (V) of male. D: Tip of long seta, showing grooved surface and apical pore (arrowed). B: Triple segment 8 (X-XII) of male, showing anteriorly-directed aesthetase. Scale bars A, E = 60 μm, B = 300 μm, C = 100 μm, D = 7.5 μm.

CHANGES IN OTHER CEPHALIC APPENDAGES. — The cephalic appendages from antennae to maxillipeds are sexually dimorphic in *E. rimana*. The antennae of the male lack setae on the coxa, basis and proximal segments of the endopod. Setation of the exopod and of the compound distal segment of the endopod is the same in both sexes. The coxal gnathobase of the mandible (arrowed in Fig. 5D) is completely atrophied in the male but well developed in the female. The biramous palp is basically the same in both sexes. The maxillule of the male is partially atrophied, with the precoxal arthrite (arrowed in Fig. 5D), coxal and basal endites and the endopod all showing marked reduction compared to the female. The exopod and coxal epipodite both retain well developed arrays of marginal setae in

both sexes. The maxilla is a well developed raptorial appendage in females but is a shrunken, wrinkled vestige in males (arrowed in Fig. 5D). The maxilliped is much smaller in the male than in the female and has a different orientation, at least when at rest (Fig. 5C). The distal part of the limb is rotated through 180° at the syncoxa-basis joint in the male only. The setation of the syncoxa is also reduced in males compared to females.

Discussion

The basal articulations between setae and antennule segments permit the setae to rotate from their resting position, to lie virtually flat against the antennule, with their tips directed toward the apex of the limb. Rotation of the setae so that they lie flat against the limb will increase streamlining and help to reduce drag. This rotation occurs when the antennules are rapidly flexed back, parallel with the body, during the initial phase of an escape response in female *E. rimana* (Yen, unpublished data). The two strongly curved, long setae on segments 7 (IX) and 8 (X-XI) have modified articulations which also allow the setae to rotate distad, but because of the curve these two setae are unable to be oriented parallel to the long axis of the limb. The basal articulations of the various setation elements of the compound apical segment also restrict the range of possible movements. In particular the anterior seta derived from segment XXVI (Fig. 5B) has an inflated integumental pad just distal to the base of the seta. As the seta rotates, the process on the setal base (arrowed in Fig. 3D) comes into contact with the integumental pad and prevents over-rotation of the seta, i.e., allowing it to rotate to lie parallel with the long axis of the limb but no farther. Rotation of the setae to lie parallel with the long axis of the limb would reduce drag.

The distribution of long setae is typical for calanoid copepods. In *Ridgewayia wilsoni* Fosshagen, for example, relatively long setae originate on segments homologous with ancestral segments V, IX, XI, XIV, XVI, XX, XXIII and XXVI (Huys and Boxshall, 1991: fig. 2.2.2B). This pattern is typical for the majority of calanoids. The presence of relatively long setae on segments homologous with these eight segments in misophrioid and cyclopoid copepods (Huys and Boxshall: figs 2.3.1A-B and 2.8.2A) indicates that this distribution of long setae may be ancestral to the entire neocopepodan grouping of orders. The relative length of the setae on segments V, IX, XI and XVI in *E. rimana* is, therefore, interpreted as an ancient copepod character. It is the modification of the ventrally-directed seta derived from segment IX and the dorsally-directed seta derived from segment XI to form a 3-dimensional array together with the straight, anteriorly-directed setae on segment V and XVI, that is novel to euchaetids.

The distribution pattern of aesthetascs in the adult female and fifth copepodid male is also typical of a wider group of calanoid copepods. The ancestral condition for calanoids is the presence of one aesthetasc on every antennulary segment (Huys and Boxshall, 1991), except the segment representing ancestral segment XXVI. In the great majority of modern calanoids this ancestral pattern is modified by loss of aesthetascs from segments. Aesthetascs are usually conserved on particular segments which serve as markers or reference points along the appendage. These conserved segments (homologous with ancestral segments VII, XI, XIV, XVI, XXI, XXV and the apical segment) are typically located immediately adjacent to key segmental boundaries that are expressed early during ontogeny (Boxshall and Huys, in press.).

The most marked qualitative change in the male antennules associated with the molt from fifth copepodid to adult is the acquisition of 19 additional aesthetascs. The addition of aesthetascs at this molt must be interpreted in a wider context within the order Calanoida. In its purest form, as expressed in male *Eucalanus attenuatus* (Dana, 1849), for example, this addition of aesthetascs at the final molt of males is equivalent to a doubling of the aesthetascs present in the female. So that segments with a single aesthetasc in adult females typically have two aesthetascs in the adult male. Huys and Boxshall (1991) speculated that "the evolutionary doubling of aesthetascs on the segments of the male antennules is correlated with the colonization of the open pelagic environment where chemical cues are of paramount importance." In male *E. rimana* this phenomenon of aesthetasc doubling is expressed in a secondarily reduced form: double aesthetascs are present only on ancestral segments II and III, and these segments lack aesthetascs in the female. Single aesthetascs, not present in the female, appear on segments 1 (I), 2 (IV) to 4 (VI), 6 (VIII) and 7 (IX), 8 (XII) and 9 (XIII), 11 (XV), 13 (XVII) to 16 (XX), 19 (XXIII) and 20 (XXIV). The addition of aesthetascs at the last molt in males is a widespread phenomenon among pelagic calanoid copepods and is not correlated with the adoption of a non-feeding strategy, such as that exhibited in *Euchaeta*.

The sexual dimorphism in the post-antennulary cephalic appendages is extreme in *Euchaeta* species and can be correlated with the non-feeding status of adult males. The pattern of reduction is clear: it is the food-handling parts of multifunctional limbs, such as the mandible and maxillule, that are reduced. The entire maxilla is atrophied, suggesting that it is almost exclusively involved in food capture and handling, with few if any secondary functions. Such morphological changes enforce the distinction in the behavior of the adult male from the female. The female continues to be highly predatory, using its enlarged maxillipeds and robust maxillae to capture and consume active prey. Recent studies (Yen et al., 1992) indicate that this copepod uses the long hair-like antennulary setae to mechanoreceptively detect fluid movements created whenever animals move through water. The prominent, paired 4-point array of setae along the antennule lie within the capture volume, defined as that volume within an approximately 1mm radial distance from the tip of the rostrum where prey, entrained within the feeding current, are captured efficiently (Doall, 1995). Lenz and Yen (1993) confirm that the long hair-like setae of the distal tip are highly mechanoreceptive and suggest that the setae at the distal tip are used for predator detection, while those within the feeding current are involved in prey detection. Further indirect support for this interpretation of the function of the proximal setae is given by the adult males which simultaneously lose several functional mouthparts as well as the 4-point setal array. The non-feeding male does not need to find prey so it sheds the prey detection system.

Mate seeking is the adult male copepod's primary goal. To suit this function, the male shifts its detection system to a new modality. The antennule is now equipped with four times as many aesthetascs. Many of these additional chemoreceptors are found within the high velocity zone of the feeding current because the sensors are in the proximal region of the antennule, close to the antennae and mandibular palp, the appendages which create the feeding current. It is significant that the antenna retains its fans of large setae on the exopod and on the bilobed distal endopodal segment. Also the mandibular and maxillulary palps are well developed in adult males, retaining fan-like arrays of long plumose setae on both rami or on the exopod and coxal epipodite respectively. Those parts of these limbs remaining in a functional state, with well developed muscles and long

fans of setae, are those involved in generating flow fields over the antennules. The adult male, therefore, retains the ability to create a scanning current across the array of sensory setae and aesthetascs distributed along the antennules. Instead of entraining prey for capture, the flow entrains signals to pass over the sensors, presumably bringing pheromones to the male's aesthetascs that can reveal the presence of the female. It is probable that the male uses these aesthetascs for mate tracking, a behavior documented for five other copepod species (Colin, 1995).

The differing orientation of the maxilliped in the adult male, the reduction in its size and the loss of enditic setation on the syncoxa all imply a change in role of the maxilliped in the adult. The maxilliped in females appears to be the primary food capture appendage (Yen, 1985), in the non-feeding adult male it may be implicated in mating and perhaps in grooming behaviors.

At the last molt from fifth copepodid to adult male changes occur to the protopodal enditic margin of the antennae, mandibles, maxillules, maxillae and maxillipeds, although the changes to maxilla involve the entire appendage. More or less extensive changes thus occur to the same part of the limbs carried on five successive cephalic and thoracic somites. It is interesting to speculate on the nature of the genetic mechanisms governing these dramatic changes in limb structure. It is possible that Hox genes may be involved in effecting the simultaneous changes in a series of five appendages since, in segmentally organized metazoans, including the crustaceans, the differential deployment of such genes is important in the control of the identity of body somites and their appendages (Akam, 1995).

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